Using Multidisciplinary Stock Identification to Optimize Morphometric Discrimination of Atlantic Herring Spawning Groups off New England

by
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ABSTRACT

Morphometric analyses of Atlantic herring (*Clupea harengus*) spawning groups off New England demonstrate how multidisciplinary stock identification can be used to optimize sampling designs and refine analytical procedures for any single approach to stock discrimination. Information on spawning areas, seasonal distribution patterns, migrations, allozymes, meristics and fishing patterns indicates that herring fisheries off southern New England in winter exploit a mix of discrete spawning groups from Georges Bank, the Gulf of Maine and the Bay of Fundy. In lieu of stock composition data from the mixed-stock fishery, the coast-wide herring resource is currently assessed as a single stock complex, and fishery managers allocate catch among summer-autumn spawning grounds and winter feeding grounds. Sampling protocols and analytical designs for recent and ongoing morphometric studies were developed using information from other disciplines of stock identification. For example, areas and seasons sampled for source specimens were determined using data on reproductive biology, geographic distributions and seasonal migrations. The number of putative stocks for developing classification functions was based on results of previous analyses of meristic and morphometric variation, allozyme data, and fishing patterns. Crossvalidation of discriminant functions indicates around 90% accuracy for classifying postspawn fish to Georges Bank, Gulf of Maine or Bay of Fundy spawning groups based on morphometric differences.

Keywords: multidisciplinary stock identification, morphometry, Atlantic herring

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INTRODUCTION

The most effective approach to identifying and discriminating fishery stocks considers various disciplines to gain multiple perspectives on complicated patterns and processes. Each discipline offers a unique view on stock structure that relates to different definitions of the term "stock" (Begg and Waldman 1999). The general "stock" definition proposed by Booke (1981): a "group of fish that maintains and sustains itself over time in a definable area" and either maintains a genetic equilibrium (a genotypic stock) or maintains "characteristics which are expressed in one or more ways depending on the type of environment" (a phenotypic stock). Fishery management also focuses on a third intraspecific group called a "harvest stock," which is a local group of fish in a continuously distributed resource that has an independent response to fishing, regardless of genetic or phenotypic similarities to adjacent resources (Gauldie 1988). Information from genetic, phenotypic, and environmental approaches can be complementary, because the definition of a stock includes all three components (Coyle 1998), and using information from multiple methods increases the likelihood that stocks are correctly identified (Hohn 1997).

"Multidisciplinary stock identification" is a relatively new approach to the challenge of understanding stock structure, and is being applied in several EU research initiatives. For example, the HOMSIR project included different molecular genetic markers, a parasitological survey, body and otolith shape analysis, tagging, analysis of life history traits, and an interdisciplinary analysis (Abaunza et al. 2000; www.homsir.com); the REDFISH project included morphometric analyses, elemental analysis of otoliths and various genetic methods (Rätz, ed. 2004; www.redfish.de); and the WESTHER project includes morphometrics, meristics, parasites, genetics, otolith microstructure, and otolith microchemistry (Hatfield et al. 2005; www.clupea.net/westher). These projects are international in scope and involve a collaborative effort among many research institutes.

A large-scale, multi-lab project is perhaps the most effective approach to determining stock structure, but is not the only way to consider multidisciplinary information. We argue that stock identification does not have to be "all or nothing," and that there is a valuable role for multidisciplinary considerations in smaller-scale research projects. The objective of this paper is to demonstrate that information from various disciplines should be evaluated to design sampling and analysis of any single-discipline study, thereby facilitating more holistic conclusions. We use recent and ongoing research on morphometrics of Atlantic herring off New England as an example.

Management of the Gulf of Maine-Georges Bank Herring Stock Complex
Western Atlantic herring (*Clupea harengus*) range geographically from Labrador to Cape Hatteras (Scott and Scott 1988; Collette and Klein-MacPhee 2002). Atlantic herring in this region are "population rich" with several separate spawning areas and discrete egg and larval distributions (Sinclair and Iles 1986, Sinclair 1988).

Most fishery management units for herring are at the scale of the stock complex, rather than at the level of the individual spawning ground (Stephenson et al. 2001). Three stock components are recognized in the Gulf of Maine region: southwest Nova Scotia-Bay of

Fundy, coastal waters of the Gulf of Maine, and Georges Bank including Nantucket Shoals (Figures 1 and 2). These three spawning groups that form the Gulf of Maine-Georges Bank Atlantic herring stock complex present a unique challenge to management. Given the intermixing of these spawning groups, and the timing of the index surveys, it is currently not possible to assess each spawning group separately. However, stock components often differ in productivity and may not support equal levels of exploitation (Smedbol and Stephenson 2001). Therefore, individual spawning components must be monitored to ensure that they are not overfished, because sustainable harvest rates may vary within the stock complex (Overholtz et al. 2004).

METHODS
Information on Stock Structure of Atlantic Herring off New England
Previous information on herring stock structure is reviewed to determine sampling strategies, character selection, analytical design and interpretation of recent morphometric studies (Armstrong and Cadrin 2001, Bolles 2005).

Geographic distribution
Spatial patterns of abundance offer an indication of stock structure. In a review of case studies that examined geographic variation in genetic composition of Atlantic cod, Ruzzante et al. (1999) concluded that examination of bathymetric features can be valuable in forming hypotheses about genetic structure of marine species. Herring spawn on relatively shallow shoals, and bathymetric features like deep channels may form boundaries among spawning groups or spawning areas. For pelagic species like herring, oceanographic features (e.g., temperature or density fronts) may also form boundaries.

Resource distribution - Fishery independent surveys indicate two distinct spawning locations: 1) inshore waters of the Gulf of Maine (Figure 3; Clark et al. 1999, Power et al. 2002, Reid et al. 1999, Tupper et al. 1998) and Georges Bank, including Nantucket Shoals and Cultivator Shoals (Figure 3; Melvin et al. 1996, Reid et al. 1999). Currently, spawning appears to be continuous from Massachusetts Bay into Great South Channel and along the northern fringe of Georges Bank to the Northeast Peak.

The distribution of adult/juvenile herring on Georges Bank and in adjacent areas changed dramatically since 1961. During the early and peak years of the Georges Bank fishery, 1961-1970, adult and juvenile herring were sparsely scattered throughout the Gulf of Maine and Georges Bank, with concentrations in the vicinity of historical spawning areas (i.e., northern edge of Georges Bank, Nantucket Shoals and in Massachusetts Bay; Melvin et al. 1996).

Although survey coverage of the inshore waters of the Gulf of Maine is generally poor, increasing numbers of herring have been collected in these areas since about 1990. Herring from the Gulf of Maine and Georges Bank overwinter between Cape Cod and Cape Hatteras, with major aggregations occurring in coastal and shelf waters off Long Island. With the recovery of the Georges Bank stock, herring have continued to broaden their winter distribution and increase in abundance in both coastal and offshore waters from Cape Cod to Cape Hatteras since 1990.

Ichthyoplankton distribution - Information on distribution of early life history stages is pertinent to stock identification because it may indicate exchange between adjacent geographic groups, or alternatively the isolation of reproductive products (Hare 2005). Annual larval surveys were conducted throughout the 1960s in the Gulf of Maine (Boyar et al. 1973a, Boyar et al. 1973b; Tibbo and Legare, 1960). Herring larvae produced by the major spawning stocks in the Gulf of Maine/Georges Bank region remain discrete during the early part of the larval stage (Sinclair and Iles 1985; Tupper et al. 1998). Therefore, the distribution pattern of young larvae (<10mm) provides information on stock structure. Based on the distribution of 4-9mm larvae, Tibbo et al. (1958) concluded that the largest herring spawning area in the Gulf of Maine occurred on the northern edge of Georges Bank. The largest herring spawning component occurred on the northeastern portion of Georges Bank.

Geographic variation
Biochemistry – If genetic differences are found among groups from different geographic areas, the groups are reproductively isolated (Carvalho and Hauser 1994). If groups are completely isolated, genetic mutations that occur in one area do not exist in another. If groups are partially isolated, different gene frequencies are maintained in each group.

Genetics have provided no conclusive evidence of discrete stock structure (Tupper et al. 1998). Biochemical methods for distinguishing herring populations in the northwest Atlantic have been conducted since the 1970s. The U.S. and U.S.S.R. biochemical and serological studies of the 1970s were considered flawed and thus no conclusions could be reached based on their information (Anthony and Waring 1980). Kornfield and Bogdonowicz (1987) found no evidence of genetically distinct herring populations in the Gulf of Maine based on mtDNA RFLP analysis.

Morphology - Genetic or environmental differences among areas can produce differences in body form among those areas that are also important for identifying phenotypic stocks (Winans, 1987). Pectoral fin ray counts were used in the past to distinguish between herring from the Maine coast, Georges Bank and Nova Scotia (Anthony and Waring 1980). The number of pectoral fin rays is related to water temperature and is determined at an early age. Adult herring from Georges Bank to Cape Cod are expected to have fewer fin rays than adults from further north since they inhabit warmer waters (Reid et al. 1999). Pectoral fin ray counts from juvenile fish from the Maine coast were found to be similar to adults from Georges Bank and Cape Cod (Anthony and Waring 1980). Libby (cited in Tupper et al. 1998) examined a number of otolith size and shape characteristics from recently hatched larvae from southwest Nova Scotia, western Georges Bank and mid-coast Maine. Eighty-four percent of otoliths were classified to the correct spawning area.

Movements and migrations
Ichthyoplankton dispersion - As mentioned above, information on distribution of early life history stages is pertinent to stock identification because it may indicate exchange between geographic groups or isolation of reproductive products. Understanding larval behavior and circulation patterns that may mix reproductive products from adjacent

spawning areas or retain larvae within an area are also important for defining stocks (Sinclair 1988).

Herring larvae produced on spawning grounds in eastern Maine and New Brunswick are transported in a westerly direction and recruit to the juvenile herring population along the Maine coast (Tupper et al 1998). Larvae from spawning grounds in the western Gulf of Maine recruit to the juvenile herring populations along the coast of central and western Maine and along the coast of New Hampshire and Massachusetts (Lazzari and Stevenson 1992, Tupper et al. 1998). Larvae produced in the Jeffreys Ledge area move inshore and disperse in all directions (Tupper et al 1998).

Georges Bank larvae may be retained in a clockwise current gyre for several months (Boyar et al. 1973a, Reid et al 1999). However, larvae from Georges Bank and Nantucket Shoals may also migrate inshore (herring younger than two years of age are not usually found on Georges Bank) (Anthony and Waring, 1980). This would most likely occur when the Georges Bank and Nantucket Shoals spawning populations are large (Tupper et al. 1998). Graham et al. (1972) report herring larvae entering the Sheepscot estuary of western Maine in the early fall, soon after hatching. In the spring, additional larvae also entered the coastal area. The authors postulate that the spring larvae originated from Georges Bank because when the Georges Bank component declined so to did the abundance of spring larvae along the coast.

Tagging observations - Movement of juveniles and adults among areas and fidelity to spawning groups is an essential element to stock identification (Harden Jones 1968). Tagging studies and fisheries data provide the background source of information on seasonal movements of adult and juvenile herring from each of the three spawning components (Figure 4). Conclusions based on this information may only apply in a general sense because herring from this region are highly migratory, are known to inter-mix throughout most of the year, vary their migration patterns from year to year, and the majority of the tagging programs were undertaken more than 20 years ago, when relative stock sizes were much different than the present. Furthermore, most of the tagging was conducted when the Georges Bank component had collapsed, and so little information is available on the seasonal movement or intermixing of this group.

The annual life cycle of Atlantic herring can be divided into five seasonal phases: overwintering, spring migration, summer feeding, spawning and fall migration. Tagging of herring at each of these stages has previously been undertaken to characterize movements and identify stocks (Stobo 1983a, b; Tupper et al. 1998). The Gulf of Maine and Georges Bank herring components are mixed to various degrees during all phases of their annual life cycle, except during spawning.

Herring tagged in the summer and fall along the Maine coast tend to move southwest and overwinter in Massachusetts Bay, although a few move south of Cape Cod and some move across the Bay of Fundy to Nova Scotia (Stobo 1983a; b; Tupper et al. 1998). Adult herring tagged off Cape Cod and the western Gulf of Maine move north and east from the central coast of Maine to southwest Nova Scotia during spring and summer (Grosslein

1986). Summer feeding adults and older juveniles (age 3) tagged in eastern Maine from 1976 to 1982 were recaptured on overwintering grounds in Massachusetts and Cape Cod Bays and in southern New England (Creaser and Libby 1988). Herring tagged in 1977 in the Great South Channel and on Jeffreys Ledge were recovered all along the northeast coast from Ipswich Bay, Massachusetts into the Bay of Fundy and along southwest Nova Scotia in the summer and autumn herring fisheries. Tagged fish were also returned during the winter fisheries in Chedabucto Bay, Cape Cod Bay and Block Island Sound (Almeida and Burns 1978, Anthony and Waring, 1980). Herring tagged in the autumn in the Bay of Fundy and off Nova Scotia migrated north to Chedabucto Bay and south to Cape Cod Bay and Block Island Sound to overwinter (Stobo et al. 1975; Stobo 1976; 1982). During the summer feeding and prespawn period, the Bay of Fundy contained a large mixture of Gulf of Maine and Bay of Fundy stocks (Stobo 1982). A herring tagging project began in 2003 to determine migration and seasonal movement patterns in the Gulf of Maine and southern New England and determine seasonal intermixing rates of spawning groups in the three existing federal management areas (Figure 2; Kanwit 2005).

In summary, the Gulf of Maine and Georges Bank contain three major spawning components from Georges Bank, Nantucket Shoals (Great South Channel area) and the coastal Gulf of Maine that are distinct but seasonally mix. As a result of mixing outside of the spawning season, much of the fishery takes place on mixed aggregations. Intermixing of components in the fishery and during resource surveys precludes separate assessment and management of the components. It is therefore necessary to evaluate the entire complex, with subsequent consideration of the individual components.

Sampling Design
Armstrong and Cadrin (2001) – Atlantic herring were collected in September 1998, on Jeffreys Ledge and Georges Bank from a commercial mid-water trawler fishing on prespawn aggregations (all fish were ripe or running ripe). Samples of postspawn herring (spent or resting) were obtained during the 1998 National Marine Fisheries Service (NMFS) Autumn Bottom Trawl Survey in October, 1998 from stations on Jeffreys Ledge and northeastern Georges Bank. An additional sample of unknown spawning affinity was obtained from the winter fishery near Block Island in southern New England during January, 1999. The sample sizes were as follows: prespawn Jeffreys Ledge, 373; prespawn Georges Bank, 416; postspawn Jeffreys Ledge, 122; postspawn Georges Bank, 103.

Bolles et al. (2005) - Herring were collected in autumn of 2003 and 2004, when the putative spawning stocks are assumed to be most discrete. Sampling was based on historical spawning time and location information. The sampling areas were the Gulf of Maine, Georges Bank, and Scots Bay and German Banks in Canada. Canadian herring were caught commercially with purse seines. The Gulf of Maine and Georges Bank herring were caught with mainly mid-water trawls. All herring were frozen. Two years of data were examined because phenotypic differences can be strongly influenced by environment and may not be temporally stable (Sinderman 1979, McQuinn 1997).

Two data sets, referred to as prespawn and postspawn, were created because changes in spawning condition can complicate morphometric analyses (Cadrin 2000, Cadrin 2005, Swain et al. 2005). The data sets were created using a quantitative method that involved obtaining total gonad weight in grams (g). Every herring whose organ weighed less than 10g were designated as postspawn. Every herring whose organ weighed greater than or equal to 10g were designated as prespawn.

2003 Data Set (prespawn n = 110; postspawn n = 139): Prespawn herring were from Scots Bay in Canada (n = 64) and from Georges Bank (n = 46). Postspawn herring were from the Gulf of Maine (n = 70) and Canada (n = 69). In 2003, no comparisons could be made between Gulf of Maine and Georges Bank herring because postspawn herring could not be collected on Georges Bank and prespawn herring could not be collected in the Gulf of Maine.

2004 Data Set (prespawn n = 341; postspawn n = 120): Prespawn herring were from Scots Bay in Canada (n = 142), from Georges Bank (n = 108), and from the Gulf of Maine (n = 91). A three way comparison was conducted on Canadian, Georges Bank, and Gulf of Maine prespawn herring. Postspawn herring were from the Gulf of Maine (n = 64) and Georges Bank (n = 56). In 2004, no comparisons could be made between Gulf of Maine and Canadian postspawn herring because postspawn herring could not be collected in Canada.

Character selection
Armstrong and Cadrin (2001) – A digital image of the sagittal view of each fish was recorded and saved. A suite of morphometric characters was measured using image analysis software. Thirty measurements were made including both traditional and truss network measurements (Strauss and Bookstein 1982; Figure 5). Sex and developmental stage were also recorded for each fish.   Otoliths were removed and imbedded in resin and aged whole using standard methods (Dery 1988).

Bolles et al. (2005) - A suite of biological data was collected including fish fork and total length (mm), fish weight (g), stomach content identification and weight (g), gonad weight (g), sex, and maturity. Sagittal otolith pairs were extracted macroscopically and put in a saturated limewater solution overnight to disintegrate membranes. Otoliths were rinsed in deionized water, blotted quickly, and allowed to dry. All herring were aged following standard aging protocols (Dery 1988).

Each non-damaged herring was positioned in the same fashion. Eight pins were inserted at pre-determined points (e.g. fin insertion points), so that they can be located easily on every fish (Cadrin 2005). Image analysis software facilitated in the identification of 19 landmarks from which 27 distance measurements were generated. The 27 distances made up the four box trusses of the "globally redundant network" defined by Strauss and Bookstein (1982). Two calibration measurements, one vertical (10 mm) and one horizontal (10 mm) were also obtained.

Analytical Design
Armstrong and Cadrin (2001) – All variables were natural log transformed prior to analysis. Data were screened for outliers by examination of bivariate scatter plots of individual variables on total length and by examination of Studentized residuals from linear regressions of each variable on total length. Additionally, a principal component analysis (PCA) was run and bi-plots of the first four principal components were examined for outliers.

Several data sets were assembled to examine different facets of morphometric variation within and between the two spawning groups. The data sets were as follows: prespawn fish collected from the commercial fishery, postspawn fish collected from the NMFS Bottom Trawl Survey, postspawn fish from Georges Bank only, and pre- and postspawn fish from Jeffreys Ledge. Reduced data sets using only the most common age in all samples were also created.

Patterns of morphometric variation were initially examined using principal component analysis (PCA). Group discrimination was accomplished using discriminant analysis on size-adjusted data. The size adjustment was accomplished using multi-group principal component analysis (MGPCA; Thorpe 1988). Size components were removed from morphometric distances by setting first component scores to zero and transforming the adjusted score matrices back to the original variable space to derive size-adjusted data matrices (Burnaby 1966, Rohlf and Bookstein 1987). Discriminant analysis with equal prior probability was performed on the size-adjusted data using jack-knifed classification. Stepwise discriminant analysis was used to select variables to use in the group discrimination. Multivariate analysis of variance (MANOVA) was used to examine shape differences among spent, resting, and immature herring in the Georges Bank postspawn sample.

Bolles et al. (2005) - PCA was used to identify patterns in the response variable (area) based on a suite of discriminating variables (distances). PCA was used to examine potential within stock variability as well as age and sex effects. MGPCA (Thorpe 1988) was used to remove the effect of fish size so that potential morphological differences could be attributed to actual shape and not size differences (Fabrizio 2005). Distance variables were analyzed with discriminant analyses (DA) and classification and regression tree analysis (CART) to determine if herring could be correctly classified to their predetermined source stock. DA was used to select the explanatory variables that would best discriminate the source herring populations. CART, the non-parametric equivalent to DA, was used to test the robustness of the DA analysis and to avoid having to meet the assumptions that are required when performing a DA.

Results
Armstrong and Cadrin (2001) –PCA of postspawn fish from Georges Bank and Jeffreys Ledge showed moderate separation along the PC1 axis (accounting for size differences between the samples) but little separation along the PC2 axis (accounting for shape variation; Figure 6). Stepwise discriminant analysis resulted in the inclusion of 15 characters, and accurately classified 88% of extrinsic samples into their correct spawning

group. Inclusion of only age-4 fish decreased the classification success to 79%. A multivariate analysis of variance (MANOVA) found no significant difference between spent, resting and immature fish in the postspawn sample from Georges Bank (Wilk's Lambda = 0.0334, p > 0.05). All univariate comparisons between these fish were non-significant for all 15 characters. This analysis indicated that using postspawn fish effectively eliminated the confounding effect of differences in spawning condition. Prespawn fish from Georges Bank and Jeffreys Ledge showed no clear separation based on PCA.   Discriminant analysis successfully classified 65% of individuals into their correct spawning group. Classification success did not improve when only age-4 fish were used.

The sample of herring from the winter fishery in southern New England was classified using discriminant function based on the postspawn data set. The sample was classified as being 70% from the Georges Bank stock and 30% from the Jeffreys Ledge stock.

Although significant morphometric differences between two spawning groups in the Gulf of Maine were found, this was the first step in the stock identification process (Cadrin 2000) culminating in the ability to assign fishery catches and survey samples to individual stocks. There are many more discrete spawning areas in the Gulf of Maine and on Georges Bank and Nantucket Shoals that have not been sampled, and the degree of morphometric variation within and between these spawning groups has yet to be determined.

Bolles et al. (2005) – Preliminary analyses indicate similar morphometric differences (Figures 7 and 8). PCA showed separation of the three main putative spawning stocks based on the suite of discriminating variables. Discriminant analyses of 2003 samples classified 85% of postspawn herring to correct spawning group, with eight variables (n = 107) and 69% of prespawn herring with four variables (n = 139). Classification tree analysis of 2003 analyses classified 87% of postspawn herring correctly with four variables (n = 107).

Discriminant analyses of 2004 samples classified 87% of postspawn herring accurately and 72% of prespawn herring. Classification and regression tree analysis also classified 87% of postspawn herring accurately and 69% of prespawn herring. All 2004 analyses were conducted with seven discriminating variables. Results did not vary considerably between sampling year, age, or sex.

DISCUSSION
These recent morphometric analyses of Atlantic herring off New England demonstrate a consideration of multidisciplinary analyses to determine sampling and analytical designs of single-discipline studies. However, similar small-scale studies are often undertaken without considering results from other studies. We advocate a more holistic approach, even for single-discipline stock identification studies.

Several aspects of single-discipline stock discriminations benefit from multidisciplinary considerations. Perhaps the most important design aspect is the number of putative

stocks. Stock composition analyses can be misleading if more spawning groups are in a mixed sample than identified in discriminant analysis. In general, fewer source groups are easier to discriminate accurately, but the presence of an unidentified group in a mixed sample can confound results. In these morphometric studies, we identified source populations and collected herring from spawning populations.

Another aspect of discriminant analysis that requires multidisciplinary consideration is the assumption of prior probabilities of group membership. Prager and Shertzer (2005) showed that stock composition analyses are sensitive to assumptions about priors. Prior probabilities are typically assumed to be either equal among groups or proportional to the group sample size in the source sample. However, alternative probabilities to these two defaults should be considered. For example, application of morphometric classifications to the winter herring fishery should consider relative abundance of spawning stocks (Overholtz 2004) and observed movement of spawning stocks to southern New England from the concurrent tagging study (Kanwit 2005) to determine prior probabilities.

Interpretation of group differences also requires a holistic perspective. The suggestion of stock structure indicated by the morphometric analyses is not supported by previous genetic studies (Kornfield and Bogdanowicz 1987, Anthony and Waring 1980). The genetic studies indicate that there is enough mixing among spawning groups to prevent fixation of distinct alleles. Therefore, the morphometric differences found in these morphometric studies may be environmentally induced. Morphometric differences may result from differences in life histories between the two groups including perhaps migration and spawning patterns, trophic differences and exposure to different environmental cues during important developmental periods. Although the spawning groups do not appear to be true genetic stocks, the presence of significant differences of morphometric characteristics indicates limited mixing of the stocks at spawning time, and the spawning groups can be treated as unit stocks for management purposes.

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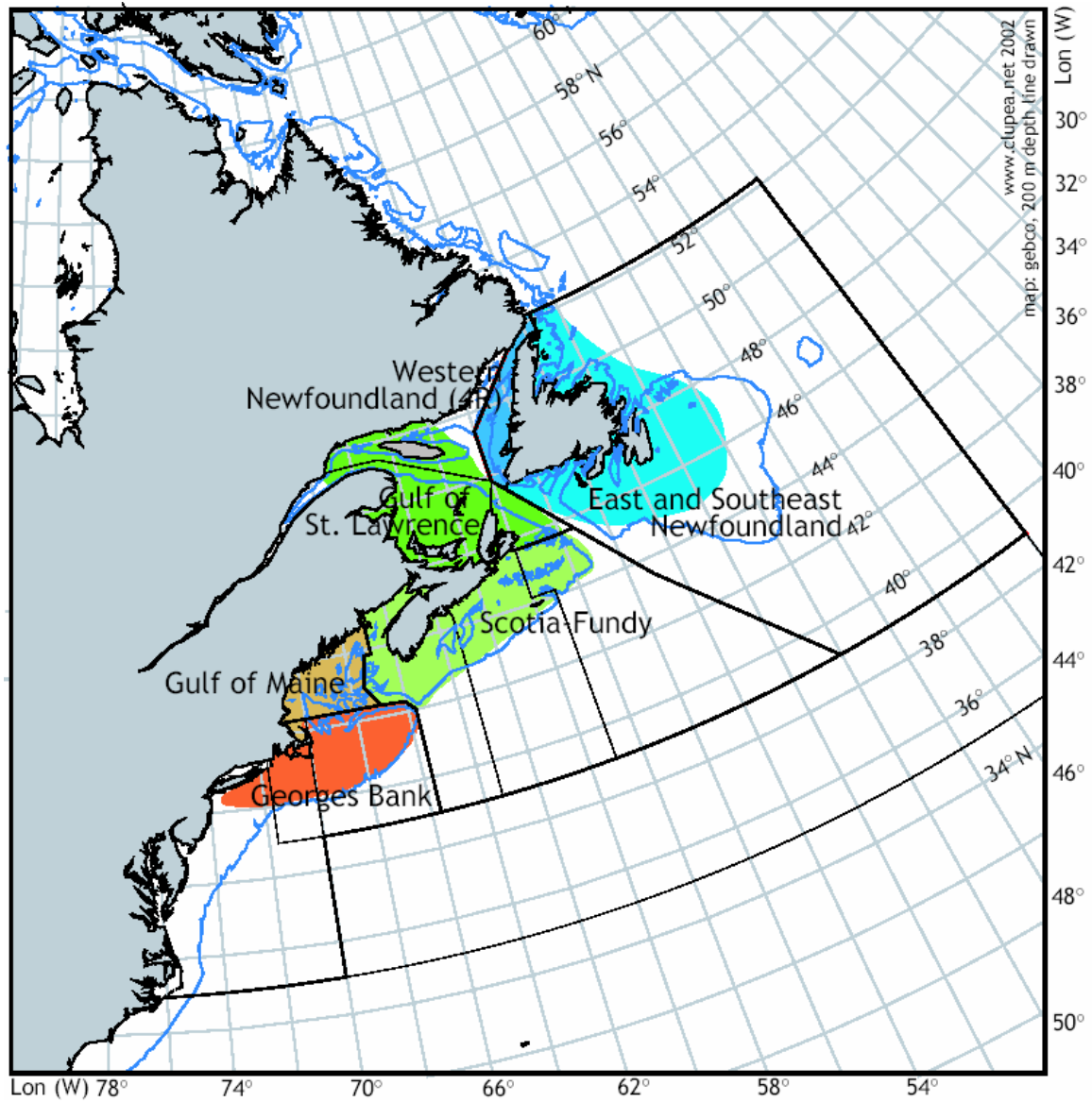Figure 1. Atlantic herring management units in the northwest Atlantic (from
www.clupea.net).

Figure 2. Current management boundaries for Atlantic herring in the Gulf of Maine and on Georges Bank and associated TACs (from Kanwit 2005).
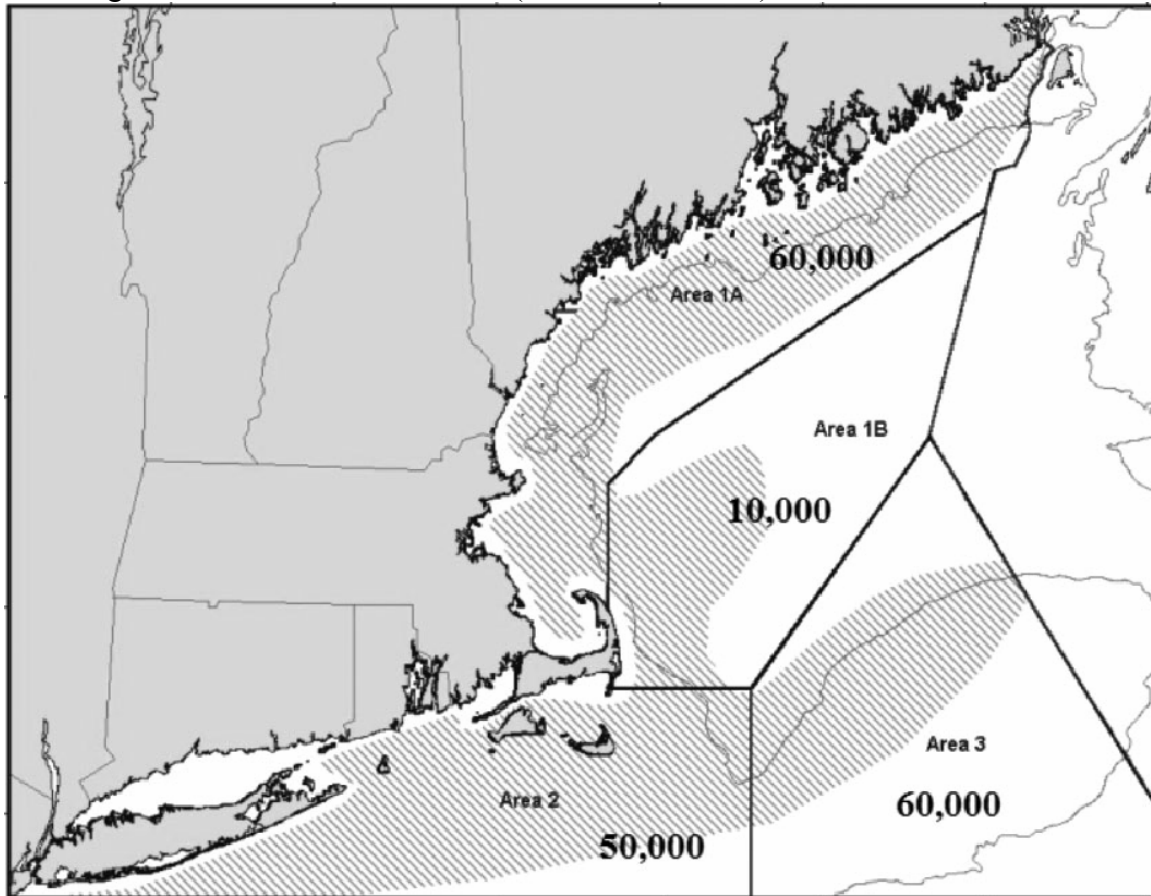
Figure 3. Generalized view of the current major herring spawning areas in the Gulf of Maine and on George Bank (from Overholtz et al. 2004).
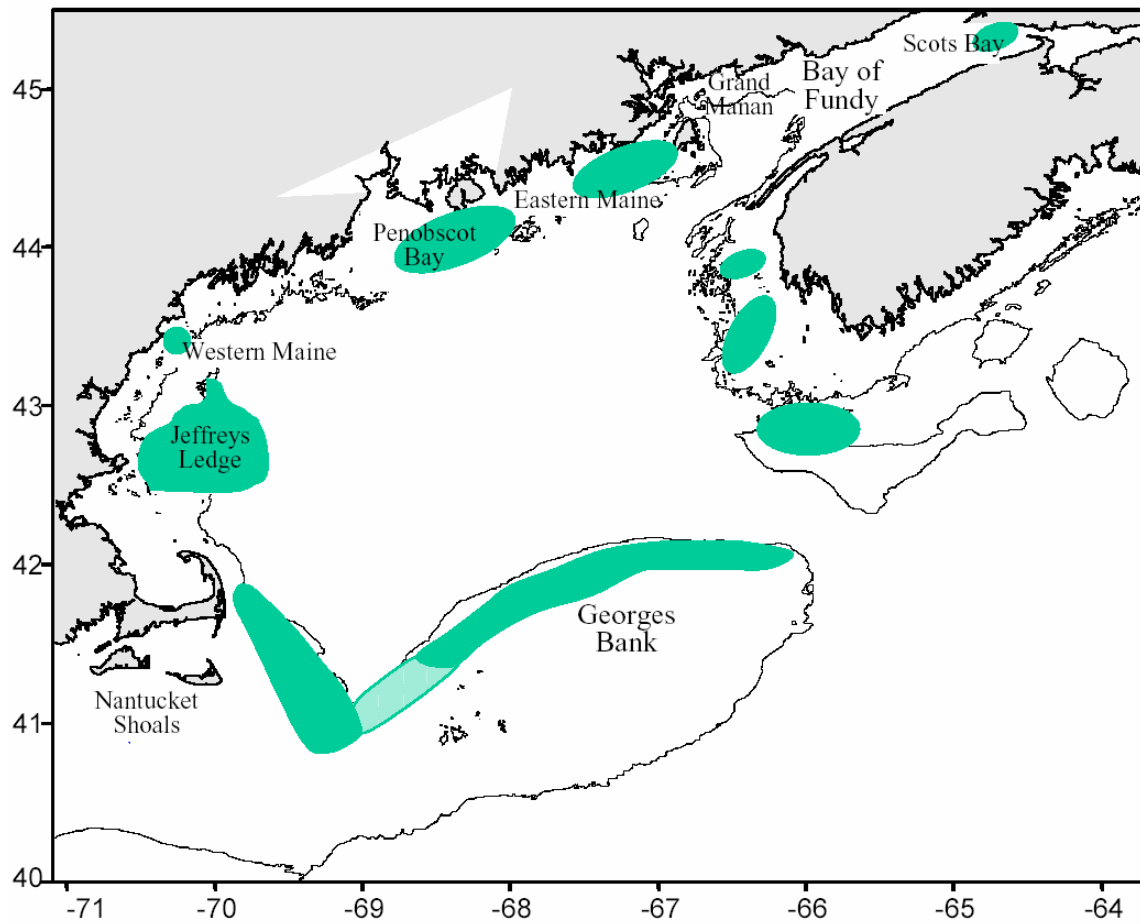
Figure 4. Hypothesized seasonal movements of three Atlantic herring spawning stocks inhabiting U.S. waters (from Reid et al. 1999).
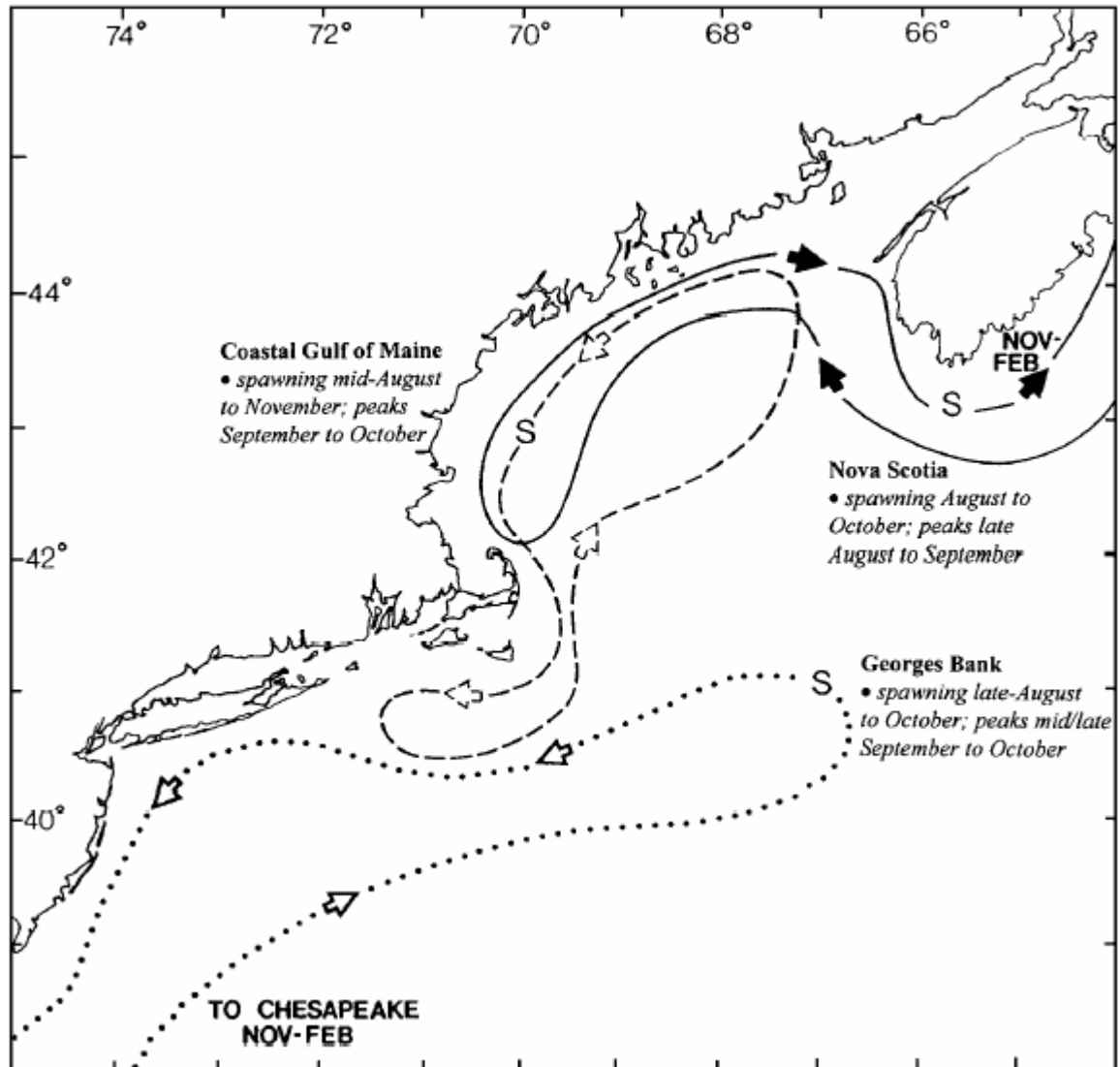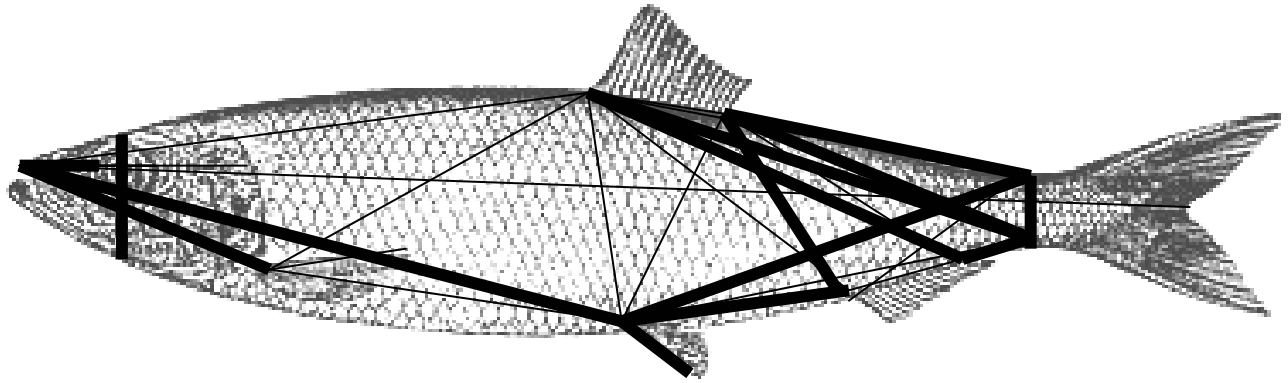
Figure 5. Morphometric features of Atlantic herring. Bold lines indicate distances used in discriminant analysis (From Armstrong and Cadrin 2001).

Figure 6. Principle component scores of Atlantic herring from postspawn aggregations on Jeffreys Ledge (Gulf of Maine) and Georges Bank (from Armstrong and Cadrin 2001).
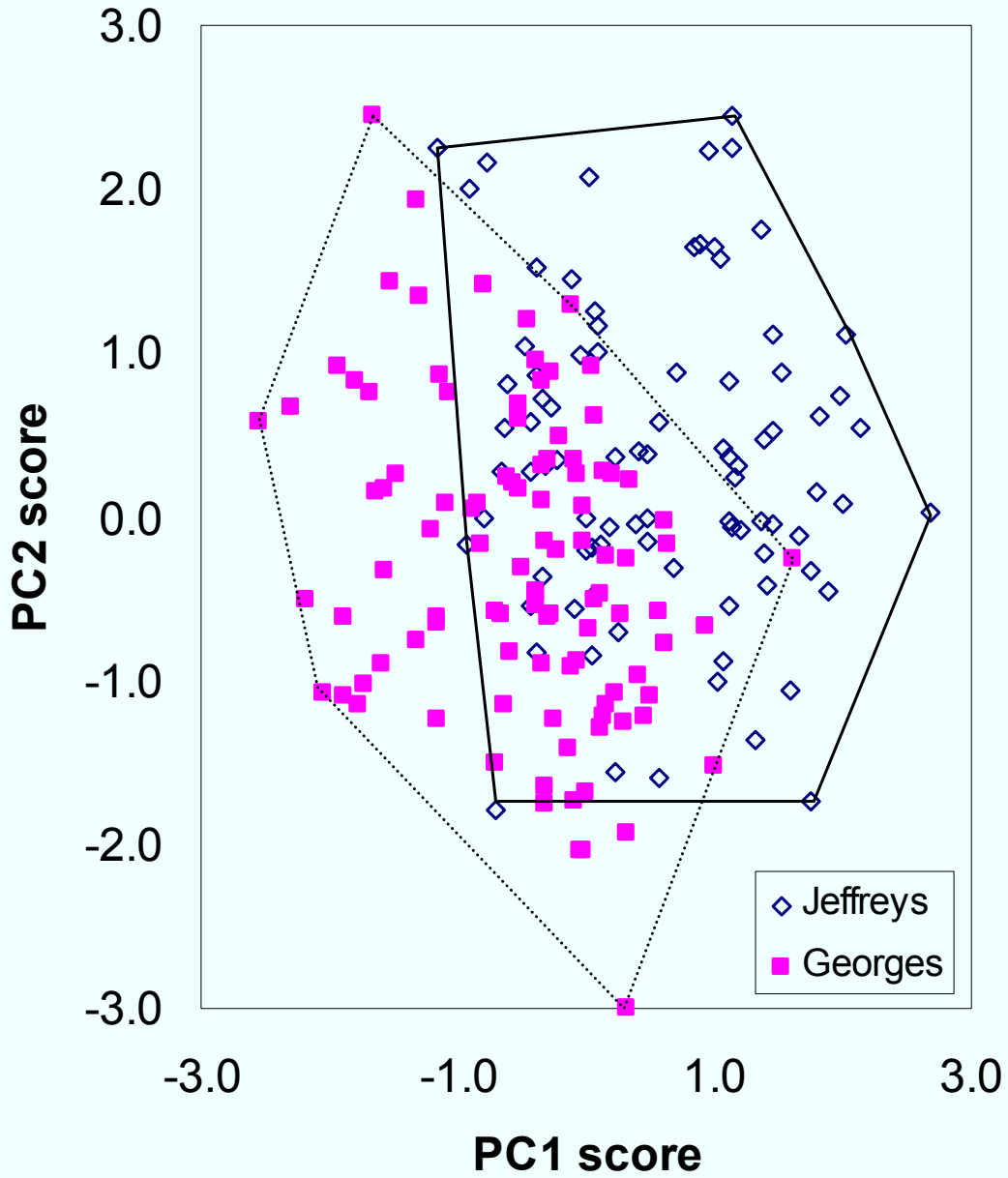
Figure 7. Principle component scores from analysis of 2004 postspawn samples (black squares: Georges Bank; red squares: Gulf of Maine) from Bolles et al. 2005.
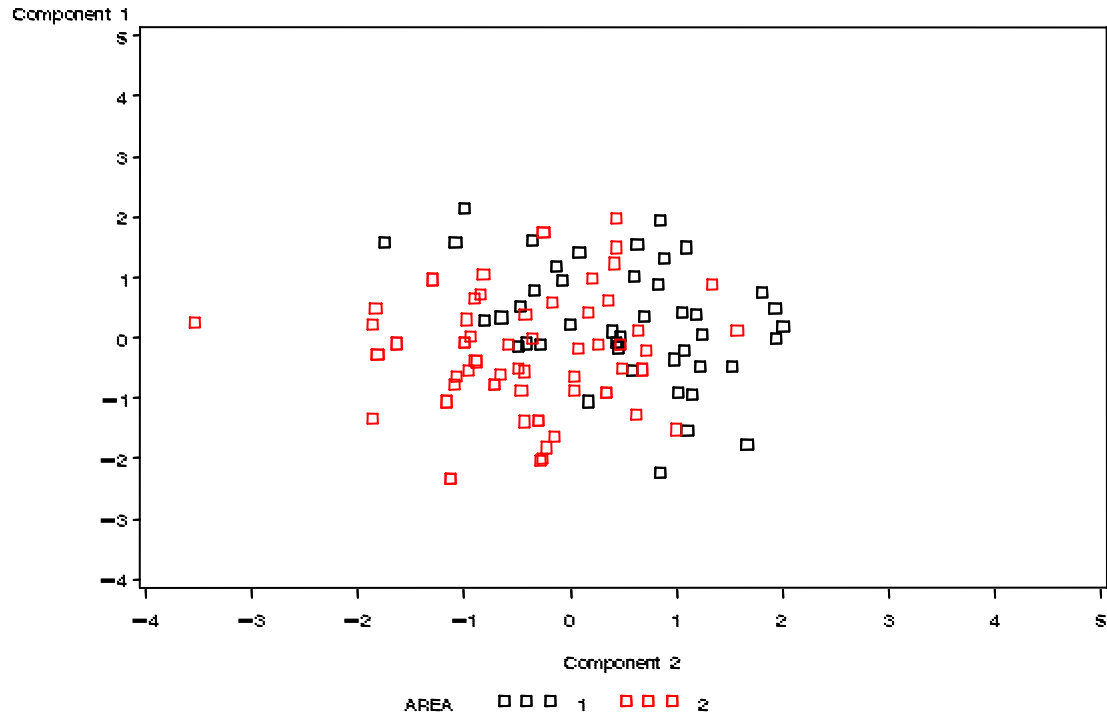
Figure 8. Discriminant scores from analysis of 2004 prespawn herring (from Bolles et al. 2005).